Biol Invasions
DOI 10.1007/s10530-011-0098-4

ORIGINAL PAPER

Humans introduce viable seeds to the Arctic on footwear

Chris Ware · Dana M. Bergstrom · Eike Müller · Inger Greve Alsos

Received: 19 August 2010 / Accepted: 26 August 2011

Abstract Expanding visitation to Polar regions combined with climate warming increases the potential for alien species introduction and establishment. We quantified vascular plant propagule pressure associated with different groups of travelers to the high-Arctic archipelago of Svalbard, and evaluated the potential of introduced seeds to germinate under the most favorable average Svalbard soil temperature (10°C). We sampled the footwear of 259 travelers arriving by air to Svalbard during the summer of 2008, recording 1,019 seeds: a mean of 3.9 (±0.8) seeds per traveler. Assuming the seed influx is representative for the whole year, we estimate a yearly seed load of around 270,000 by this vector alone. Seeds of 53 species were identified from 17 families, with Poaceae having both highest diversity and number of seeds. Eight of the families identified are among those most invasive worldwide, while the majority of the species identified were non-native to Svalbard. The number of seeds was highest on footwear that had been used in forested and alpine areas in the 3 months prior to traveling to Svalbard, and increased with the amount of soil affixed to footwear. In total, 26% of the collected seeds germinated under simulated Svalbard conditions. Our results demonstrate high propagule transport through aviation to highly visited cold-climate regions and isolated islands is occurring. Alien species establishment is expected to increase with climate change, particularly in high latitude regions, making the need for regional management considerations a priority.

Keywords Alien · Non-indigenous · Dispersal · Germination · Human-mediated dispersal · Propagule pressure

C. Ware · E. Müller · I. G. Alsos (✉)
The University Centre in Svalbard (UNIS), PO Box 156, 9171 Longyearbyen, Norway
e-mail: inger.g.alsos@uit.no

D. M. Bergstrom
Australian Antarctic Division, Department of the Environment, Water, Heritage and the Arts, 203 Channel Highway, Kingston 7050, Australia

I. G. Alsos
Tromsø University Museum, 9037 Tromsø, Norway

Introduction

Until recently in the high-Arctic and Antarctic, two processes have maintained ecological integrity: low frequency of human-mediated dispersal, and the prevailing climate, both of which are rapidly changing (Convey et al. 2006; Elven et al. 2011). Seed dispersal by humans and cargo is to some degree documented for the Antarctic (Whinam et al. 2005; Frenot et al. 2005; Lee and Chown 2009a, b; SCAR 2010), and has been the subject of management

Published online: 20 September 2011

development by the Antarctic Treaty Parties (Australia and SCAR 2007). In contrast, no such quantification exists for the Arctic, where few biosecurity measures are currently employed.

The total number of archaeophytic, persistent, and transient alien plants in the Arctic is low, constituting a very low to zero proportion of the regional Arctic floras (Elven et al. 2011). Exceptions exist in some of the millennium-old Viking settlements and more recent Russian settlements where non-indigenous plants are more prevalent. In some Arctic settlements, sometimes very far to the north, casual introductions are quite frequent (Liška and Soldán 2004; Elven et al. 2011). For other taxa, records of established alien species exist, although these are also few. A vole is known to be established on Svalbard (Fredga et al. 1990) while the first records of a non-native crustacean and species of kelp have been made at lower Arctic latitudes (Ashton et al. 2008).

Elsewhere in the world, humans and their associated activities have been demonstrated to be effective vectors of unintentional species transfer, providing carriage for plants (Clifford 1956; Powell 1968; Falinski 1972; Higashino et al. 1983; Whinam et al. 2005; Lee and Chown 2009a; Wichmann et al. 2009), arthropods (McCullough et al. 2006; Hughes et al. 2010), bacteria (Curry et al. 2002; Drake et al. 2007; Hughes et al. 2010; McNeill et al. 2011), terrestrial vertebrates (Gillespie 1985), and marine organisms (Carlton 1985; Gollasch 2002). Generally, the little amount of research concerning invasion processes in the Arctic is biased towards post-invasion—a trend identified globally (Puth and Post 2005). To date, the only attempt to quantify the significance of a pathway of species introduction to the Arctic focused on ship-mediated introductions to Alaska (Hines and Ruiz 2000).

Human activity in the Arctic has rapidly increased over the past 40 years (Kaltenborn 2000; Forbes et al. 2004). Between 1995 and 2004 there was a 255% increase in the number of tourists visiting Svalbard (Governor of Svalbard 2006), while Greenland recorded a 500% increase over the same time period (Statistics Greenland 2009). While the tourism sector is increasing rapidly, so too are other travel sectors such as that associated with science. Polar scientists often visit and work in several alpine or high latitude environments, and may move frequently between them (e.g. Whinam et al. 2005), increasing the chances of introducing organisms pre-adapted to Arctic environmental conditions.

While dispersal is a critical step in species invasions, the Arctic climate also presents a significant barrier to species colonization (Alsos et al. 2007). The effect of climate on new species colonization is complex, and varies at different stages of colonization (Shevtsova et al. 2009). For plants, the initial bottleneck of colonization may be germination. Low temperatures have been shown to limit germination in Arctic plant species (Sørensen 1941, Müller et al. 2011) suggesting also that germination of introduced alien plant species would be similarly impaired. Despite this, many temperate grassland, shrub and herbaceous species have been shown experimentally to be capable of germination at surface temperatures commonly recorded in the Arctic today (Baskin and Baskin 1998; Trudgill et al. 2000). Indeed, Arctic summer surface temperatures can be several degrees warmer than those reported from meteorological stations recorded at two meters above the surface (Scherrer and Körner 2010). Furthermore, it is possible that seeds introduced today, capable of lying dormant in soil for many years (Thompson et al. 1997), may be capable of germination under future climates.

Alien plants are widely documented at higher latitudes (Alaska, sub-Antarctic), and are relatively easy to monitor and identify (compared to e.g. bacteria, arthropods, fungi). For these reasons, and due to the incomplete knowledge of other taxonomic groups in the Arctic (Coulson and Refseth 2004; Elvebakk and Prestrud 1996; Alsos et al. 2009), plant seeds make appropriate exemplars to investigate the extent to which new species could be transported to, and survive in, Arctic regions. Humans can carry a high plant propagule load on footwear (Clifford 1956; Powell 1968; Falinski 1972; Higashino 1983; Whinam et al. 2005; Lee and Chown 2009a; Wichmann et al. 2009; McNeill et al. 2011), from which seeds can disperse (Lee and Chown 2009a; Wichmann et al. 2009; Pickering and Mount 2010; Ware and Bergstrom, unpublished data), and as such, humans are likely to introduce alien seeds while traveling. Here, by using footwear as a pathway of introduction, we investigated the threat of species transfer to Svalbard. We asked the following questions: (1) What is the size and composition of the seed load being carried to Svalbard on travelers' footwear? (2) What factors explain the number of seeds on footwear? (3) Could seeds transported to Svalbard on footwear germinate under current Svalbard conditions? Based on the results of these investigations, implications for management are discussed.

Methods

Location

Around 60% of the Svalbard archipelago (74°–81°N and 10°–30°E) is covered in ice, leaving coastal pockets suitable for vegetation (Jónsdóttir 2005). Three of the five Arctic bioclimatic subzones identified by Walker et al. (2005) are present in Svalbard: polar desert (subzone A), northern Arctic tundra (subzone B) and middle Arctic tundra (subzone C). Mean air temperatures of the warmest month in each zone respectively are between 1–2.5°C, 2.5–4°C, and 4–6°C (Elvebakk 2005). There are 165 native plant species (Alsos et al. 2011). Around 60 non-indigenous plant species have been recorded around the main settlements (Liška and Soldán 2004), of which around 28–37 are established or are frequently re-introduced (Elven and Elvebakk 1996; Elven et al. 2011).

Most travelers to Svalbard travel by plane, arriving at the major airport located in Longyearbyen, on the island of Spitsbergen. During 2008, 68,901 travelers flew into Longyearbyen (Governor of Svalbard, personal communication) with more than 90 % of these typically arriving over the tourist season (March–September) (Governor of Svalbard 2006). Many travelers join expedition ships at the local port, exploring the archipelago by ship.

Footwear sampling

We sampled the footwear of 259 travelers arriving at Svalbard Airport between 20 June and 28 September 2008. Around 75% of travelers arriving in Svalbard were wearing footwear with soles capable of carrying substantive quantities of soil, such as those typical of hiking/running shoes (Ware, unpublished data); only these travelers were asked to participate in the survey. We scraped off any soil attached to participants' footwear using a stiff-bristled brush and forceps, scrubbed the shoe sole, and inspected the shoe lacing and tongue for biological material. Footwear was cleaned until all visible material was removed, and material was collected in plastic bags. A sampling unit was considered as a pair of shoes and in instances where travelers arrived with two pairs of shoes (i.e. one pair in their luggage) the second pair was considered a separate sample. In between samples, sampling equipment was cleaned thoroughly and visually inspected for dirt and propagules so as to avoid sample contamination. Samples were tagged with unique identifiers. We sorted samples into the following categories with the aid of a dissecting microscope (3×): seeds; plant and invertebrate fragments (bryophyte fragments, leaves, macroscopic invertebrate parts); soil (organic material); and non-organic material (highly variable, but commonly including metal and plastic fragments, chewing gum, and feathers). Total seed and bryophyte fragment numbers were tallied. Seeds were identified to the lowest taxonomic group possible using an identification guide (Cappers et al. 2006) and online resources (Kirkbride et al. 2006). Families were crosschecked against the most invasive families listed within the Global Invasive Species Database (ISSG 2010). While bryophyte fragments collected may have been capable of vegetative growth, we excluded these from substantive analysis due to the difficulties associated with their identification (e.g. Rowntree et al. 2010). We considered a focus on vascular plants to be a priority, owing to their significance in the global invasive flora (e.g. ISSG 2010). Soil samples were stored at −20° prior to sample sorting, and weighed following sorting using Metter Toledo scales.

Germination

We placed collected seeds on filter paper (grade 1, Whatman, Maidstone, UK) moistened with distilled water via a wick attached to a reservoir. Seeds were then kept in a phytotron chamber at 10°C, under 24-h light (approximately 40 µmol m^{-2} s^{-1} at seed surface, 35 W fluorescent tube, 840 HE (Osram, Munich, Germany)) to simulate ambient average summer soil conditions in Svalbard. A temperature of 10°C was selected as this best reflects average soil surface records from a number of favorable Svalbard sites; the temperature was fixed as this reflects the relatively low standard temperature deviation recorded from these sites (Müller, unpublished data).

Seeds were monitored for germination (protrusion of a radical) for 48 days.

Traveler statistics

Participants also completed a questionnaire (linked to their footwear sample using a unique identifier), categorizing themselves as a tourist, scientist, businessperson, resident, or student. Furthermore, they indicated whether, and when, they had last cleaned their footwear; whether they had used their footwear in the 3 months prior to traveling; and in what type of habitat they had used their footwear (forested, alpine, rural, or urban areas) over the three previous months.

Statistical analysis

To determine the relationship between the weight of soil collected from footwear and the number of seeds found, we fitted a generalized linear model (GLM) with a quasipoisson error distribution and logarithmic link function, and an overdispersion characteristic. From this, we also calculated seeds per 1 g of soil. To test for correlation between seed load and the two explanatory variables, traveler categories and previous footwear use, we fitted GLMs separately. Again, we fitted the GLMs using a quasipoisson error distribution with a logarithmic link function and an overdispersion characteristic. We began by fitting maximum models containing all predictor variables and interaction terms. Model simplification was then achieved by removing variables and interaction terms stepwise. Model fit was assessed using analysis of variance (ANOVA) tests to determine whether simplified models significantly increased deviance; the significance of difference was assessed using F tests. Where deviance was not increased (i.e. $P < 0.05$), variables or interaction terms were omitted from further modeling. To determine the effectiveness of traveler footwear cleaning prior to travel, we used the Wilcoxon rank sum test with continuity correction. For all mean values calculated in our analyses, standard errors were also calculated (±SE).We used the statistical and programming package R (version 2.10.0, R Development Core Team 2008) to carry out all analyses.

Results

Footwear samples

Overall, 40% of the 259 footwear samples examined contained seeds. A total of 1,019 seeds were collected representing a mean of 3.9 (±0.8) seeds per traveler, or 9.9 (±1.1) seeds per traveler that had seeds attached to their footwear. The maximum number of seeds found in a single sample was 117 (Table 1), and 26 samples (10%) contained 10 or more seeds. In addition, we also found 465 bryophyte fragments in the samples representing a mean of 1.8 (±0.6) fragments per traveler. A mean of 0.27 g (±0.06) of soil was found on a pair of footwear, with a range: 0–9.9 g (35% of footwear did not contain any soil). The amount of soil present on footwear was significantly correlated with the number of seeds present (F = 165, $P < 0.05$, 166 *df*). Where soil was present in a sample, there was an average of 2.9 ± 1.2 seeds per gram of soil. We did not find any live invertebrates, eggs, or larvae in the samples.

Table 1 Summary of footwear samples, and survey information collected from travelers arriving to Svalbard

Traveler category	n	% Contaminated	% With soil	Total seeds	Mean seeds	Bootstrapped 95% CI	Max. seeds per sample	% Cleaned
Tourist	170	41	69	631	3.71	2.3, 6.6	117	21
Scientist	37	57	65	212	5.73	2.8, 12.0	62	19
Student	28	36	46	98	3.50	1.1, 9.1	39	21
Business	19	47	63	59	3.11	1.0, 7.7	25	10
Resident	5	20	40	19	3.80	0.0, 7.6	19	0
Total	259	48	65	1,019	3.93	2.8, 6.1	–	20

CI confidence interval

The majority of the identified seeds collected were grasses (60%), with 17 Poaceae species identified (Table 2). Other seeds present were tree, herb and sedge seeds, with a proportion (13%) unable to be identified (Fig. 1). Four of the herb species and three grass species identified from our samples have already established as alien species in Svalbard. Only two possible native species were found (Table 2).

Germination

Of the total 1,019 seeds tested for germination, 266 (26%) germinated under the test conditions. *Taraxacum* sp. (n = 9)*, Cerastium brachypetalum* (n = 8), *C. glomeratum* (n = 12), and *Dactylis glomerate* (n = 2) all recorded 100% germination, while *Deschampsia flexuosa, Poa annua* and *P. trivialis* all recorded germination >40% (Table 2).

Traveler statistics

Category of traveler arriving to Svalbard had no significant effect on the number of seeds imported on footwear (Table 1). Twenty percent of participants reported cleaning their footwear prior to travel: of this percentage, 49% contained seeds. There was no evidence that footwear cleaning by participants lowered the number of seeds transported on shoes ($W = 5{,}615.5$, $P > 0.05$).

Fifty seven per cent of the participants had used their footwear in forests, while 30% had used their footwear in alpine regions (Fig. 2). A GLM that included use of footwear in both forested and alpine areas provided the best fit to the data (Table 3), demonstrating that footwear previously used in these two habitats contained a significantly higher seed load ($F = 11.06$, $P = 0.001$, 257 *df*).

Discussion

This study demonstrates that people arriving in Svalbard pose an identifiable hazard to the local environment through the introduction of alien plant seeds that are capable of germination even under current climatic conditions. Travelers are providing the means to increase the plant species pool capable of reaching the Arctic, a trend identified already in the sub-Arctic (Carlson and Shephard 2007). The seed load per person transferred to the Arctic is similar to that being introduced by expeditioners to the Antarctic, and the same types of species are being transported (Lee and Chown 2009a). Our findings support those of others demonstrating that humans are capable of translocating many of the world's widespread alien plant species (Pickering and Mount 2010).

Our analysis demonstrated that footwear previously used in forested or alpine areas carried significantly higher numbers of seed than that used in rural or urban areas. Few studies have attempted to investigate previous use as a factor predisposing an item to contamination. McNeill et al. (2011) found golfing footwear to be the most highly contaminated item in a study of the footwear of arriving airplane passengers in New Zealand, while Whinam et al. (2005) found many Antarctic expeditioners had recently used their clothing in natural environments. The positive relationship between outdoor use and clothing and equipment contamination is logical, and our study reaffirms the notion that these items provide the greatest biosecurity hazard.

The strong association between the presence of soil and incidence of seeds and bryophyte fragments is consistent with other studies (Hughes et al. 2010; McNeill et al. 2011), and highlights the potential for any clothing and equipment capable of carrying soil to mediate alien organism introduction. The mean number of seeds found per gram of soil reported here (2.9 ± 1.2) is comparable to that found in soil attached to the footwear of arriving aircraft passengers to New Zealand (2.5 ± 0.37 per 1 g soil—McNeill et al. 2011). As with McNeill et al. (2011), our seed counts may be underestimated owing to imperfect visual searches in our samples, while counts would be slightly inflated by the few occasions where seeds were found in the absence of soil (e.g. on footwear lacing or tongue).

The sampled seed load contained a number of cosmopolitan species, and eight of the 17 families identified belonged to those families ranked as most invasive at a global scale (Pyšek 1998). Considering the dominance of Poaceae seeds found in connection with other human-mediated seed dispersal studies (e.g. Schmidt 1989; Hodkinson and Thompson 1997; Lee and Chown 2009a), and the wide geographic range of establishment that some Poaceae species

Table 2 Number of seeds of native or alien species found on traveler's footwear arriving in Svalbard, and seed germination percentages

Group and family	Taxa	Native	Alien	Unidentified species	Life form	% Germination
Gymnosperm						
Cupressaceae	*Thuja plicata*		1		P	
Angiosperms—dicotyledons						
Apiaceae	*Torilis japonica*		1		A	
Asteraceae[a]	Unidentified			1		
	Taraxacum sp.[b]		**9**		P	100
Betulaceae	*Betula pubescens*		143		P	1
Brassicaceae[a]	Unidentified			1		
	Erucrastrum sp.		1			
	Isatis sp.		7			
	Nasturtium microphyllum		23		P	9
Caryophyllaceae	Unidentified					
	Cerastium brachypetalum		8		A	100
	Cerastium glomeratum		12		A	100
Ericaceae	*Vaccinium* sp.			5		
Fabaceae[a]	*Astragalus glycyphyllos*		1		P	
	Medicago falcata		1		A/P	
Papavaceae[a]	Unidentified			1		
	Papaver sp.			3		
Plataginaceae	*Plantago major*		**27**		P	7
Polygonaceae	Unidentified			4		100
	Polygonum aviculare		**3**		A/P	
	Rumex sp.			**1**		
	Rumex crispus		1		P	
Ranunculaceae[a]	*Ranunculus* sp.			1		
	Ranunculus acris		**5**		P	
Rosaceae[a]	*Geum macrophyllum*		1		P	
	Geum rivale		1		P	
Angiosperms—monocotyledons						
Cyperaceae	*Carex* sp.			14		
	Carex acutiformis		1		P	
Juncaceae[a]	Unidentified			3		
	Juncus sp.			6		
	Juncus effuses		10		P	60
	Juncus pygmaeus		22		A	
Juncaginaceae	*Triglochin maritima*		20		P	
Poaceae[a]	Unidentified			73		4
	Agrostis sp.			**1**		100
	Agrostis stolonifera		24		P	38
	Alopecurus pratensis		**6**		P	50
	Ammophila arenaria		2		P	50
	Bromopsis sp.		1			
	Bromus sp.		2			

Table 2 continued

Group and family	Taxa	Native	Alien	Unidentified species	Life form	% Germination
	Bromus hordeaceus		4		A	75
	Calamagrostis pseudophragmites		2		P	
	Dactylis glomerata		2		P	100
	Deschampsia sp.			1		
	Deschampisa caespitosa		**3**		P	
	Avenella flexuosa		89		P	45
	Festuca sp.			21		5
	Festuca lemanii		1		P	100
	Festuca rubra	1			P	
	Holcus lanatus		1		P	100
	Hordeum sp.			**2**		50
	Lolium perenne		2		A/P	50
	Phleum pratense ssp. *pratense*		2		P	
	Phleum pratense ssp. *serotinum*		1		P	
	Poa sp.			41		39
	Poa annua		**36**		A	58
	Poa trivialis		180		P	57
	Poa pratensis	62			P	10
	Trisetum flavescens		3		P	
Unidentified seeds				118		7
Totals		63	663	293		26

Numbers in bold indicate those alien species that have already established on Svalbard. Life form: perennial (P), annual (A) or both (A/P) according to www.plants.usda.gov

[a] Families that are those identified as the most invasive worldwide (as per Pyšek 1998) or families with a high number of invasive species (ISSG 2010)

[b] *Taraxacum* sp. are not currently listed as a Svalbard alien, but are present in the Russian settlement of Pyramiden (Ware, pers. obs.) and Barentsburg (Alsos, pers. obs.)

have achieved (i.e. *Poa annua* and *Poa trivialis* have both established in the Antarctic—Frenot et al. 2005; Hughes et al. 2010), the finding that Poaceae seeds dominated our samples was not unexpected.

Our relatively high germination rates indicate that germination may not be a barrier to establishment in Svalbard for many non-indigenous species. Germination occurred rapidly under the test conditions, with 87% of those that germinated doing so within 14 days, and the remainder within 48 days—well within the growing season. These germination results are based on present climatic means; however, temperature increases of 0.61°C per decade are expected for the period 1961–2050 (Hanssen-Bauer 2002) which would likely favour the germination of more northerly plants if introduced to Svalbard (e.g. Trudgill et al. 2000; Milbau et al. 2009).

Further improving the chances of successful establishment are the few samples that contained many propagules. One sample contained over 100 seeds, and 26 samples had 10 or more seeds (10%). If these were dispersed into suitable habitat, the effects of propagule pressure would increase the likelihood of their successful establishment (i.e. Williamson 1996; Lockwood et al. 2005, 2007; Colautti et al. 2006). Similarly, where seeds are pre-adapted to the Svalbard climate, the potential for establishment is greater. Many participants had used their footwear in either northern boreal forested regions or alpine regions, and many of the species identified from shoe samples are found in these habitats.

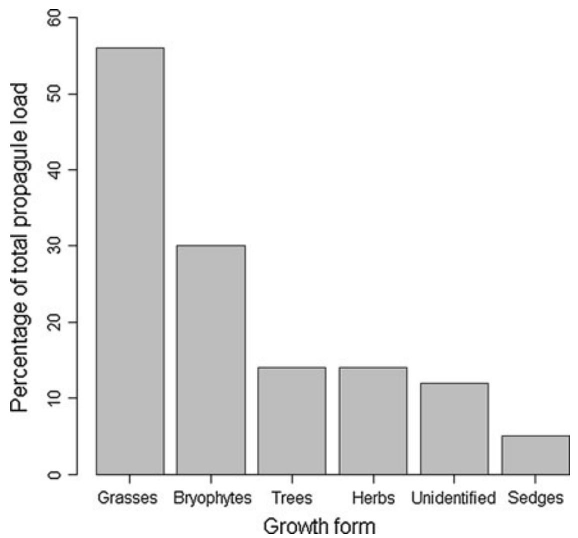

Fig. 1 Percentage of total propagules by growth form collected from the footwear of travelers to Svalbard

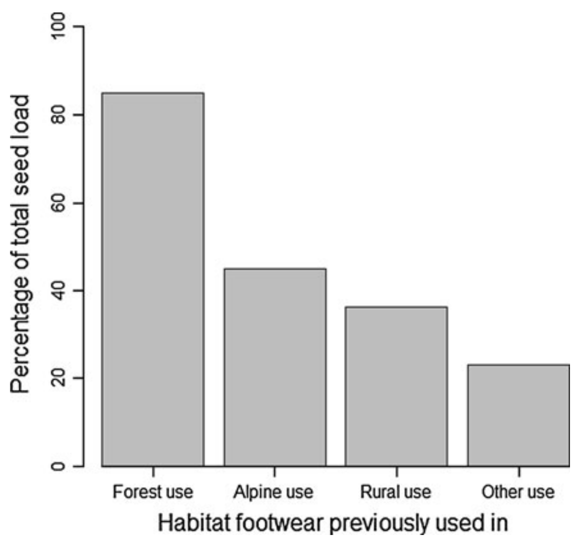

Fig. 2 Percentage of total seeds by previous use collected from the footwear of travelers to Svalbard

While we would expect these species to be better adapted to the challenges of establishing in Svalbard, establishment of other more generalist species cannot be precluded. Indeed, *Barbarea vulgaris* ssp. *arcuata* and species of the *Tarxacum ruderalia* aggregate—both generalist European natives—have established on Svalbard and are spreading locally (Alsos, pers. obs.).

As our data were collected over a summer period, they were not suited to testing the effects of seasonality on seed load (no data were collected during winter or spring). There was however, a large variation in seed loading (see CIs—Table 1), and our models failed to account for parts of this variation (Table 2). Factors such as footwear use at times of seed production and dispersal may then be important considerations in more precisely modeling human-mediated seed influx to Svalbard.

While recognizing the above caveat, it is possible to project an estimate of a yearly seed load introduced on footwear based on visitor numbers alone. For the year of the study (2008) 68,901 people arrived at the Svalbard airport, equating to an estimated yearly seed load of 270,000 from travelers' footwear alone. In addition, approximately 30,000 cruise ship passengers land on Svalbard. In a separate preliminary study we sampled the footwear of three hundred cruise ship passengers landing on Svalbard and found just 21 seeds and bryophyte fragments (Ware, unpublished data), suggesting that cruise ship passengers may contribute a smaller propagule load to the region. Many other pathways of species introduction to Svalbard exist, including cargo, planes, scientific equipment and the clothing and personal equipment of travelers (e.g. Whinam et al. 2005; Barnes et al. 2006; Lee and Chown 2009a, b). From these, organisms of other taxa may be transferred. Thus, the total propagule load being introduced to Svalbard would be considerably higher than estimated here.

Table 3 The results of ANOVA tests comparing different generalized linear models investigating the effects of where footwear had been previously used (forest, alpine, rural or urban habitats) on the number of seeds affixed to footwear

Model variables	Deviance residuals (max–min)	Deviance on *df*	Δ Deviance	*P*
Seeds = forest × alpine × rural × other	(−5.0398 to 2.8748)	2,932.4 on 244	–	–
Seeds = forest + alpine + rural + other	(−4.249 to 2.876)	3,294.4 on 254	−362.00	0.1325
Seeds = forest + alpine + rural	(−4.076 to 2.892)	3,314.6 on 255	−20.2	0.4263
Seeds = forest + alpine	(−3.8360 to 3.1327)	3,331.0 on 256	−16.4	0.4785
Seeds = forest	(−3.423 to 3.423)	3,370.6 on 257	−39.6	0.272

Management implications

Our study suggests that modern aviation, as the means by which tourism has achieved its rapid increase, has the potential to increase the pressure of plant species introduction to highly visited cold-climate regions and isolated islands globally. Studies elsewhere demonstrate that footwear and the soil attached to it are furthermore capable of carrying a variety of other taxa (e.g. McNeill et al. 2011). While we found no evidence that footwear could transport live invertebrates, eggs, or larva, we did not analyze collected samples for the presence of bacteria or fungi which may have been present. The question of whether alien plants can establish on Svalbard requires further investigation (being dependent on a variety of factors including soil moisture, aspect, and season); however, our germination results, and the artificial ranges achieved by other introduced plants at high latitudes, suggest that a more conservative approach to regional biosecurity need be considered if the ecological and genetic integrity of the local flora is to be maintained. As many other organisms can be transported in association with soil, measures taken to reduce the seed load imported to Svalbard will also reduce the hazard of other organisms being introduced.

Measures to address the introduction of seeds via footwear exist. The ineffectiveness of footwear cleaning by travelers participating in this study suggests that educating travelers of the need to clean footwear prior to arrival may not be effective alone. While the effectiveness of educating Antarctic expeditioners to clean footwear and personal equipment of seeds and contaminants was apparent (Bergstrom, pers. obs.), this may have been due to the combination of follow-up inspections. Beyond education, more stringent management measures could include the adoption of a biosecurity policy at entry points to Svalbard, such as those in place in New Zealand (Biosecurity New Zealand 2010), and for Antarctic tour operators (IAATO 2010). Any management interventions in Svalbard would ideally be positioned within a more comprehensive framework, incorporating all pathways and vectors of introduction, and all organisms, especially pathogens.

Our study makes a case for a more precautionary approach to the management of alien species in Svalbard. The pathway analysis described here suggests that more non-indigenous plant species can be expected in Svalbard if measures to prevent their introduction are not considered. Moreover, our study implies that isolated islands or regions worldwide, which are experiencing similar increases in human traffic as is occurring in Svalbard, may be exposed to similar hazards or even greater hazards if climate is less of a limiting factor.

Acknowledgments We thank the many people who assisted in footwear sampling at the Svalbard airport, and the 259 participants who kindly gave up their shoes for cleaning after arrival. We would also like to thank the staff at the Svalbard Airport for allowing us to conduct the study on airport premises. Financial assistance for this project was received from the Svalbard Environmental Protection Fund. This project is closely aligned with the IPY Aliens in Antarctica Project. Finally, we wish to extend our thanks to three anonymous reviewers for their comments on the manuscript.

References

Alsos IG, Eidesen PB, Ehrich D, Skrede I, Westergaard K, Jacobsen GH, Landvik J, Taberlet P, Brochmann C (2007) Frequent long-distance plant colonization in the changing Arctic. Science 316:1606–1609

Alsos IG, Gillespie L, Marusik YM (2009) Arctic islands, biology. In: Gillespie R, Clague DA (eds) Encyclopedia of Islands. University of California Press, Berkeley

Alsos IG, Arnesen G, Sandbakk BE, Elven R (2011). http://svalbardflora.net. Accessed 20 Aug 2011

Ashton GV, Riedlecker EI, Ruiz GM (2008) First non-native crustacean established in coastal waters of Alaska. Aquat Biol 3:133–137

Australia and SCAR (Scientific Committee on Antarctic Research) (2007) IPY Aliens in Antarctica. Information paper presented by the Government of Australia and the Scientific Committee on Antarctica Research: information paper 49. Antarctic Treaty Consultative Meeting (ATCM XXX), New Dehli

Barnes DKA, Hodgson DA, Convey P, Allen CS, Clarke A (2006) Incursion and excursion of Antarctic biota: past, present and future. Glob Ecol Biogeogr 15:121–142. doi: 10.1111/j.1466-822x.2006.00216.x

Baskin CC, Baskin JM (1998) Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego

Biosecurity New Zealand (2010) Entering New Zealand. New Zealand Government, New Zealand. http://www.biosecurity.govt.nz/enter. Accessed 6 May 2010

Cappers RTJ, Bekker RM, Jans JEA (2006) Digital seed atlas of the Netherlands. Groningen archaeological studies 4. Barkhuis Publishing, The Netherlands

Carlton JT (1985) Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Mar Biol Ann Rev 23:313–371

Carlson ML, Shephard M (2007) Is the spread of non-native plants in Alaska accelerating? Meeting the challenge: invasive plants in Pacific Northwest ecosystems. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR

Clifford HT (1956) Seed dispersal on footwear. Proc Bot Soc Br Isles 2:129–131

Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. Biol Invasions 8:1023–1037. doi:10.1007/s10530-005-3735-y

Convey P, Frenot Y, Gremmen N, Bergstrom DM (2006) Biological invasions. In: Bergstrom DM, Convey P, Huskies AHL (eds) Trends in Antarctic terrestrial and limnetic ecosystems: Antarctica as a global indicator. Springer, The Netherlands, pp 194–220

Coulson SJ, Refseth D (2004) The terrestrial and freshwater invertebrate fauna of Svalbard (and Jan Mayen). In: Prestrud P, Strøm H, Goldman H (eds) A catalogue of the terrestrial and marine animals of Svalbard. Norsk Polarinstitutt 201, pp 57–122

Curry CH, McCarthy JS, Darragh HM, Wake RA, Todhunter R, Terris J (2002) Could tourist boots act as vectors for disease transmission in Antarctica? J Travel Med 9:190–193

Drake LA, Doblin MA, Dobbs FC (2007) Potential microbial bioinvasions via ships' ballast water, sediment, and biofilm. Mar Poll Bull 55:333–341

Elvebakk A (2005) A vegetation map of Svalbard on the scale 1:3.5 mill. Phytocoenologia 35:951–967

Elvebakk A, Prestrud P (1996) A catalogue of Svalbard plants, fungi, algae and cyanobacteria. Norsk Polarinstitutt 198, pp 1

Elven R, Elvebakk A (1996) Part 1. Vascular plants. In Elvebakk A, Prestrud P (eds) A catalogue of Svalbard plants, fungi, algae, and cyanobacteria. Norsk Polarinstitutt 198, pp 9–55

Elven R, Murray DF, Razzhivin V, Yurtsev BA (2011) Checklist of the panarctic flora (PAF). CAFF/University of Oslo, Oslo. http://gbif.no/paf. Accessed 20 Aug 2011

Falinski JB (1972) Anthropochory in xerothermic grasslands in the light of experimental data. Acta Soc Bot Pol 41: 357–368

Forbes BC, Monz C, Tolvanen A (2004) Ecological impacts of tourism in terrestrial polar ecosystems. In: Buckley R (ed) Environmental impacts of ecotourism. CAB International, Oxfordshire, pp 155–170

Fredga K, Jaarola M, Ims RA, Steen H, Yoccoz NG (1990) The 'common vole' in Svalbard identified as *Microtus epiroticus* by chromosome analysis. Polar Res 8: 283–290

Frenot Y, Chown SL, Whinam J, Selkirk PM, Convey P, Skotnicki M, Bergstrom DM (2005) Biological invasions in the Antarctic: extent, impacts and implications. Biol Rev 80:45–72. doi:10.1017/s1464793104006542

Gillespie GD (1985) Hybridization, introgression, and morphometric differentiation between Mallard (*Anas platyrhynchos*) and Grey Duck (*Anas superciliosa*) in Otago, New Zealand. The Auk 102:459–469

Gollasch S (2002) The importance of ship hull fouling as a vector of species introductions in to the North Sea. Biofouling 18:105–121

Governor of Svalbard (2006) Report on tourism statistics from Svalbard 1997–2006. Svalbard Sysselmannen. http://www.sysselmannen.no/hovedEnkel.aspx?m=45275. Accessed 10 Mar 2009

Hanssen-Bauer I (2002) Temperature and precipitation in Svalbard 1912–2050: measurements and scenarios. Polar Rec 38:225–232

Higashino PK, Guyer W, Stone CP (1983) The Kilauea wilderness marathon and crater rim runs: sole searching experiences. Newsl Hawaii Bot Soc 22:22–28

Hines AH, Ruiz GM (2000) Biological invasions at cold-water coastal ecosystems: ballast- mediated introductions in Port Valdez/Prince William Sound. Final Report to Regional Citizens Advisory Council of Prince William Sound

Hodkinson DJ, Thompson K (1997) Plant dispersal: the role of man. J Appl Ecol 34:1484–1496

Hughes K, Lee J, Ware C, Kiefer K, Bergstrom D (2010) Impact of anthropogenic transportation to Antarctica on alien seed viability. Polar Biol 33:1125–1130. doi:10.1007/s00300-010-0801-4

IAATO (International Association of Antarctica Tour Operators) (2010) Boot, clothing and equipment decontamination guidelines for small boat operators. IAATO. http://www.iaato.org/guidelines.html. Accessed 30 May 2010

ISSG (Invasive Species Specilist Group) (2010) Global invasive species database. http://www.issg.org/database/welcome/disclaimer.asp. Accessed 3 June 2010

Jónsdóttir IS (2005) Terrestrial ecosystems on Svalbard: heterogeneity, complexity and fragility from an arctic island perspective. Proc Roy Ir Acad 105B:155–165

Kaltenborn BP (2000) Arctic-alpine environments and tourism: can sustainability be planned? lessons learned on Svalbard. Mt Res Dev 20:28–31

Kirkbride JH Jr, Gunn CR, Dallwitz MJ (2006) Family guide for fruits and seeds. United States Department of Agriculture, Washington, DC. http://nt.ars-grin.gov/sbmlweb/OnlineResources/frsdfam/Index.cfm. Accessed 12 May 2010

Lee JE, Chown SL (2009a) Breaching the dispersal barrier to invasion: quantification and management. Ecol Appl 19: 1944–1959. doi:10.1890/08-2157.1

Lee JE, Chown SL (2009b) Quantifying the propagule load associated with the construction of an Antarctic research station. Antarct Sci 21:471–475. doi:10.1017/S0954102009990162

Liška J, Soldán Z (2004) Alien vascular plants recorded from the barentsburg and pyramiden settlements, Svalbard. Preslia 76:279–290

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends Ecol Evol 20:223–228

Lockwood JL, Hoopes MF, Marchetti MP (2007) Invasion ecology. Blackwell, Malden, USA, pp 59–76

McCullough DG, Work TT, Cavey JF, Liebhold AM, Marshall D (2006) Interceptions at nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. Biol Invasions 8:611–630

McNeill M, Phillips C, Young S, Shah F, Aalders L, Bell N, Gerard E, Littlejohn R (2011) Transportation of nonindigenous species via soil on international aircraft passengers' footwear. Biol Invasions. doi:10.1007/s10530-011-9964-3

Milbau A, Graae BJ, Shevtsova A, Nijs I (2009) Effects of a warmer climate on seed germination in the subarctic. Ann Bot 104:287–296

Müller E, Cooper EJ, Also IG (2011) Germinability of arctic plants is high in perceived optimal conditions but low in the field. Botany 89:337–348

Pickering C, Mount A (2010) Do tourists disperse weed seed? a global review of unintentional human-mediated terrestrial seed dispersal on clothing, vehicles and horses. J Sustain Tour 18:239–256. doi:10.1080/09669580903406613

Powell RH (1968) Harmful plant species entering New Zealand 1963–1967. NZ J Bot 6:396–401

Puth LM, Post DM (2005) Studying invasion: have we missed the boat? Ecol Lett 8:715–721

Pyšek P (1998) Is there a taxonomic pattern to plant invasions? Oikos 82:282–294

R Development Core Team (2008) R 2.7.2. A language and environment. Vienna, Austria. Available from http://cran.r-project.org

Rowntree JK, Cowan RS, Leggett M, Ramsay MM, Fay MF (2010) Which moss is which? Identification of the threatened moss Orthodontium gracile using molecular and morphological techniques. Conserv Genet 11:1033–1042

SCAR (Scientific Committee on Antarctic Research) (2010) Preliminary results from the International Polar Year Program: Aliens in Antarctica. Working paper 4 presented to the Committee on Environmental Protection. Antarctic Treaty Consultative Meeting XXXIII, Punta del Este, Uruguay

Scherrer D, Körner C (2010) Infra-red thermometry of alpine landscapes challenges climatic warming projections. Global Change Biol 16:2602–2613

Schmidt W (1989) Plant dispersal by motor cars. Vegetatio 80:147–152

Shevtsova A, Graae BJ, Jochum T, Milbau A, Kockelbergh F, Beyens L, Nijs I (2009) Critical periods for impact of climate warming on early seedling establishment in subarctic tundra. Global Change Biol 15:2662–2680

Sørensen T (1941) Temperature relations and phenology of the northeast greenland flowering plants. Commission for Scientific Research in Greenland, Copenhagen

Statistics Greenland (2009) Flight passenger statistics. Department of Finances, Greenland. http://www.stat.gl/Statistik/Turisme/tabid/99/language/en-US/Default.aspx. Accessed 19 Jan 2010

Thompson K, Bakker JP, Bekker RM (1997) The soil seed banks of north west Europe: methodology, density and longevity. Cambridge University Press, Cambridge

Trudgill DL, Squire GR, Thompson K (2000) A thermal time basis for comparing the germination requirements of some British herbaceous plants. New Phytol 145:107–114

Walker DA, Raynolds MK, Daniels FJA, Einarsson E, Elvebakk A, Gould WA, Katenin AE, Kholod SS, Markon CJ, Melnikov ES, Moskalenko NG, Talbot SS, Yurtsev BA (2005) The circumpolar arctic vegetation map. J Veg Sci 16:267–282

Whinam J, Chilcott N, Bergstrom DM (2005) Subantarctic hitchhikers: expeditioners as vectors for the introduction of alien organisms. Biol Conserv 121:207–219

Wichmann MC, Alexander MJ, Soons MB, Galsworthy S, Dunne L, Gould R, Fairfax C, Niggemann M, Hails RS, Bullock JM (2009) Human-mediated dispersal of seeds over long distances. Proc Roy Soc Lond B 276:523–532. doi:10.1098/rspb.2008.1131

Williamson M (1996) Biol invasions. Chapman & Hall, London, pp 28–52